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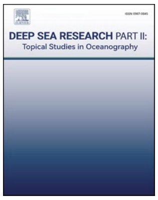

The impacts of El Niño Southern Oscillation on the pelagic fish community structure of the northern Humboldt Current system

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ABSTRACT

The northern Humboldt Current System (HCS) is a highly productive eastern boundary upwelling system off Peru. El Niño Southern Oscillation (ENSO) is one of the main drivers of short-term climate variability, whose warm (El Niño) and cold (La Niña) phases can trigger changes in the physical, chemical, biological, and socioeconomic conditions of the northern HCS. We explored the impacts of ENSO phases and magnitude in the region over the structure of the pelagic fish community in the northern HCS through the study of spatial and temporal beta diversity changes. To achieve this goal, we used 25-year taxonomic composition data from pelagic scientific surveys and statistical multivariate methods. We found that, depending on the magnitudes, most of the El Niño (EN) categories substantially increased the diversity index values in this system with respect to the neutral phase. In contrast, La Niña (LN) decreased it. The community spatial structure principally showed three ecological regions, which varied in extension, indicator species, and composition across ENSO phases. The local contribution to beta diversity (LCBD) showed that the shelf break is essential in shaping the community structure among ENSO phases. The changes in temporal beta diversity suggest that the spatial structure or change of the community abundance is influenced by the magnitude of the EN phase. We conclude that the oceanographic changes caused by the ENSO phases may significantly impact the fish community structure in the northern HCS. Our results are relevant to implementing climate-ready management measures in this ecosystem.

1. Introduction

In marine ecosystems, fluctuations in environmental conditions, like rising temperatures, can affect the habitat and behaviour of marine fish, leading to changes in biodiversity patterns (e.g., Hu et al. (2022)). These environmental effects may be direct, influencing the physiology of organisms, or indirect, affecting lower trophic levels and creating a cascading effect throughout the food web (Lehodey et al. 2020). In addition to natural factors, anthropogenic processes — such as fishing, pollution, and habitat degradation — also impact marine biodiversity, often resulting in significant biodiversity losses (Worm et al. 2006).

The Humboldt Current System (HCS) is an eastern boundary upwelling system (EBUS) located in the east Pacific Ocean, off the coasts of Peru and Chile (Chavez et al. 2008). Along the Peruvian coast, trade winds blowing toward the equator generate a persistent coastal upwelling of cold and nutrient-rich waters (Swartzman et al. 2008), which led to high primary productivity (Tarazona and Arntz 2001; Pennington et al. 2006; Chavez and Messié 2009), characterising the HCS with anomalously high biological productivity in terms of fish per unit area when compared with other EBUS (Chavez and Messié 2009). This elevated productivity supports diverse fisheries, such as the Peruvian anchoveta (Engraulis ringens) (Chavez et al. 2008), which sustains one of the largest monospecific fisheries in the world (FAO 2020). In addition, the HCS also features a shallow and intense Oxygen Minimum Zone (OMZ) (Graco et al. 2017), which shapes the habitat of several pelagic species (Bertrand et al. 2011; Salvatteci et al. 2022).

Due to its low-latitude location, the HCS exhibits significant variability and susceptibility to interact with extreme inter-annual system disturbances (Bakun and Weeks 2008). El Niño Southern Oscillation (ENSO) and its warm phase, El Niño (EN), is the leading interannual fluctuation in the HCS (Gutiérrez et al. 2016; Bonino et al. 2019). The EN is a climate phenomenon characterized by the warming of the surface

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waters in the tropical Pacific Ocean and the weakening of equatorial trade winds (Timmermann et al. 2018). This warm phase triggers changes in the circulation of ocean currents and the thermocline and oxycline depths, with an increase in water temperature and a decrease in upwelling (Bertrand et al. 2020), thereby reducing primary productivity (Barber and Chavez 1983; Arntz et al. 2006; Chavez et al. 2008; Espinoza-Morriberón et al. 2019; Bertrand et al. 2020; Lehodey et al. 2020). In contrast, La Niña (LN) is the cold phase of the ENSO, producing an anomalous increase in upwelling and expansion of cold waters, favouring the habitat of Peruvian anchoveta and other species associated with cold conditions (e.g., red squat lobster (Yapur-Pancorvo et al. 2023)). EN events in the HCS have been more recurrent in the last decade, producing changes in the ocean conditions and species dwelling therein, as well as causing socioeconomic consequences (Thompson et al. 2017; Kluger et al. 2019; Bertrand et al. 2020; Pécastaing and Chavez 2020; Gutiérrez and Bouchon 2021).

Given their economic and ecological roles, the Peruvian anchoveta and other pelagic fishes such as the chub mackerel (Scomber japonicus) and the jack mackerel (Trachurus murphyi), have been the main target species of several studies in the HCS during the last decades (Alegre et al. 2013, 2015; Torrejón-Magallanes et al. 2021). However, other species that inhabit the pelagic environment and contribute to the fish species diversity in this system have been studied less extensively. It has been stated that latitudinally richness tends to be greater in the northern tropical areas compared to southern temperate regions (Vildoso B. et al. 1999). Across trophic levels, more species diversity has been found in groups of higher (e.g., birds, sharks) and lower levels (e.g., diatoms, dinoflagellates) compared to the intermediate levels (e.g., small pelagic species) (Fréon et al. 2009). There is also evidence of latitudinal variations in the diversity of fishes off Chile, which decreases as one moves to southern areas (Navarrete et al. 2014).

Several studies have shown that the extreme EN event of 1997–1998 caused significant changes in the pelagic fish community. Bouchon et al. (2001) used fishery-dependent data to investigate fish diversity in the northern HCS from 1994 to 1998, finding that during the preceding and subsequent years to the extreme EN event, the region had low fish diversity with a large dominance by the Peruvian anchoveta and high biological productivity. They also found that the EN 1997–1998 increased fish diversity due to the migration of tropical species and reduced the anchoveta dominance. Other studies indicated that tropical and oceanic fish, including tunas and mackerels, were more prevalent during the 1997–1998 event (Espino 1999; Ñiquen and Bouchon 2004). Also, other studies have found that these interannual migration of species depend on the magnitude of environmental changes and the species composition during the period before the development of the phenomenon (Bertrand et al. 2004; Chavez et al. 2008; Lehodey et al. 2020). Nonetheless, there is a lack of information on how different ENSO events have impacted pelagic fish diversity and structure in the northern HCS in the last two decades.

This study investigated the variations in the community composition and spatial structure of pelagic fishes in response to distinct ENSO events in the northern HCS. Using a long-term and fishery-independent dataset collected by scientific surveys from 1995 to 2019 off the Peruvian coast, we quantify the diversity changes in the pelagic community over space caused by the three main ENSO phases: El Niño, La Niña and neutral (spring and summer). We focus our analyses on identifying alpha and beta diversity changes among ENSO phases and species indicators of ENSO events. To our understanding, this is the first study that statistically assesses the diversity of fishes in the pelagic habitat in the northern HCS and the impacts of several ENSO events.

2. Materials and methods

2.1. Survey data

We used taxonomic data from the pelagic acoustic scientific surveys conducted by the Marine Institute of Peru (IMARPE) off the Peruvian coast from 1995 to 2019. These surveys were carried out twice a year, during the austral summer and spring seasons, from 3° to 18°S and to a maximum distance of 100 nautical miles (NM) from shore (Castillo et al. 2009). The survey design is systematic, following parallel and equidistant cross-shore transects of ~100 NM long and with ~10–15 NM inter-transect spacing (Castillo et al. 2009) (Fig. S1). These acoustic surveys investigated various components of the Peruvian marine ecosystem, such as oceanographic conditions and the geographic distribution, biomass, and abundance of the Peruvian anchoveta and other pelagic species with economic importance to provide management advice (Castillo et al. 2009; IMARPE 2020).

Taxonomic data come from mid-trawl samplings conducted during surveys (~150–200 trawls per survey) at depths between ~10 and 100m using a fine mesh net with a 43 mm diagonal mesh size. Trawl locations are decided during the vessel trajectory based on the echoes detected by the scientific echo-sounders (Fig. S1). The main goal of the trawls is to determine the species composition, size spectra, and biological information of the species that produced the echoes. Since strong echoes are mostly sampled, this approach increases the probability of effectively representing the species that inhabit the system. Even though trawl locations cover the entire survey area, they are unevenly distributed over space and are usually denser in coastal areas. Fishery biologists conducted the taxonomic identification of all specimens caught in a trawl, recording their mass (kg), body size and biological information. More information regarding the survey sampling protocol can be found in Castillo et al. (2009).

2.2. Data standardization

Due to differences in the survey area coverage, we only used trawl information between 5° and 16°S and from 0 to 80 NM from the shoreline. While several marine taxa are caught in the mid-water trawls, we constrained analyses to fish taxa. We also performed a taxonomic standardization (see Supp Information – Appendix A) to produce homogeneous and comparable taxonomic data since the taxonomic sufficiency (i.e., the ability of surveyors to identify an organism up to the species level) might have varied among surveys. After taxonomic standardization, we used 67 fish taxa (Table S2) in our analyses. Finally, we standardized the catch per taxa by dividing it by a measure of fishing effort (trawling time in minutes), producing a catch per unit effort (CPUE) per taxa, which was then used as a proxy for abundance.

2.3. ENSO phase classification

To study the impacts of the ENSO phases on the diversity of fishes in the northern HCS, our primary analyses classified the ENSO events by phase and intensity following the Coastal El Niño Index (ICEN) (Takahashi et al. 2014). The ICEN is established by the Commission in charge of studying the El Niño Phenomenon (ENFEN) in Peru. This index measures the variability of the regional climate in the eastern equatorial Pacific Ocean, and it is determined by calculating the three-month moving average of the sea surface temperature (SST) anomaly in the Niño 1 + 2 region (off Ecuador and Peru). More information about the ICEN can be found at ENFEN (2024).

For the Neutral phase, we assigned surveys based on the months they were conducted: i) Neutral Summer (N_Summ): surveys from December to April; Neutral Spring (N_Spring): from July to October. We divided the El Niño phase into four categories based on intensity: EN extreme (EN_extreme), EN strong (EN_strong), EN moderate (EN_moderate), and EN weak (EN_weak). For the La Niña phase, we considered three categories: LN strong (LN_strong), LN moderate (LN_moderate), and LN weak (LN_weak), for a total of nine ENSO categories. For the study period, the EN_extreme corresponds to the EN 1997–1998 event, the EN_strong to the EN 2015–2016 event, and the EN_moderate to the Coastal EN 2017 event. Information from trawl surveys conducted during the same ENSO phase category was aggregated (Table 1) and used in the analyses described below.

There is also an alternative ENSO classification based on the Ocean Niño Index (ONI) in the Niño-3+4 region in the central Pacific (5°S–5° N, 170°–120° W). Therefore, we also conducted complementary analyses based on this classification. For this case, the ENSO phases are: i) Central Pacific El Niño (EN_CP), ii) Eastern Pacific El Niño (EN_EP), iii) Extreme El Niño (EN_extreme), iv) Coastal El Niño (EN_coastal), and v) La Niña Strong (LN_strong). Following this criterion, we had seven ENSO categories, including the neutral ones. The discrimination of surveys for each category was done following the information found in Bertrand et al. (2020) (Table 1).

Table 1
List of surveys from 1995 to 2019 used in this study. Information on the start date, end date, and number of trawls is also shown. Surveys were grouped into distinct ENSO categories by ICEN and ONI indices.

Year	Name	Begin Date (Month)	End Date (Month)	N° trawls	ENSO phase (ICEN)	ENSO phase (ONI)
1995	C9502-04	2	4	93	N_Summer	CP_EN
	C9508-09	8	9	76	N_Spring	N_Spring
1996	C9602-04	2	4	93	LN_Strong	N_Summer
	C9608-09	8	9	79	LN_Strong	N_Spring
	C9611-12	11	12	67	LN_Strong	N_Summer
1997	C9702-04	2	4	80	N_Summer	N_Summer
	C9709-10	9	10	85	EN_extreme	EN_extreme
1998	C9803-05	3	5	102	EN_extreme	EN_extreme
	C9805-06	5	6	50	EN_extreme	EN_extreme
	C9808-09	8	9	128	EN_extreme	LN_strong
	C9811-12	11	12	80	N_Summer	LN_strong
1999	C9902-03	2	3	94	N_Summer	LN_strong
	C9909	9	9	24	N_Spring	LN_strong
	C9911-12	11	12	132	LN_Weak	LN_strong
2000	C0001-02	1	2	197	N_Summer	LN_strong
	C0010-11	10	11	135	N_Spring	N_Spring
2001	C0103-04	3	4	145	N_Summer	N_Summer
	C0107-08	7	8	151	LN_Weak	N_Spring
	C0108-09	8	9	71	LN_Weak	N_Spring
	C0110-11	10	11	234	LN_Weak	N_Spring
2002	C0202-03	2	3	103	EN_Weak	N_Summer
	C0208	8	8	77	N_Spring	EP_EN
	C0209-11	9	11	172	N_Spring	EP_EN
2003	C0302-04	2	4	96	N_Summer	EP_EN
	C0305-06	5	6	43	LN_Mod	–
	C0308-09	8	9	87	N_Spring	N_Spring
	C0310-12	10	12	50	N_Spring	N_Spring
2004	C0402-03	2	3	181	N_Summer	N_Summer
	C0408-09	8	9	75	N_Spring	CP_EN
	C0411-12	11	12	62	N_Summer	CP_EN
2005	C0502-03	2	3	159	N_Summer	CP_EN
	C0508-09	8	9	51	LN_Mod	N_Spring
	C0511-12	11	12	60	LN_Mod	N_Summer
2006	C0602-04	2	4	117	N_Summer	N_Summer
	C0608-09	8	9	27	EN_Weak	EP_EN
	C0611-12	11	12	113	EN_Weak	EP_EN

(*continued on next page*)

2.4. Global analysis

Fig. 1 shows the spatial distribution of trawls considered for each ENSO phase. We calculated three types of taxonomic diversity indices: 1) alpha diversity, which represents local diversity and was calculated by averaging the taxonomic richness (i.e., the number of taxa) by trawl; 2) gamma diversity, which represents the global diversity of a study area and represents the total number of taxa; and 3) beta diversity was calculated to estimate how the community changes among the trawls. Total beta diversity (BD_{Total}) was calculated using the beta.div function of the adespatial R package (Dray et al. 2022). The BD_{Total} statistic used in this paper is the total variance of the Hellinger-transformed community composition data matrix. The Hellinger transformation is effective for abundance data as it assigns lower weights to species with low CPUE and many zeros (Legendre and Gallagher 2001), particularly true for taxonomic survey data. Because the community data were Hellinger-transformed, BD_{Total} values range between 0 and 1 for any community study, and the BD_{Total} statistics are comparable among communities (Legendre and De Cáceres 2013). The maximum value of BD_{Total} does not depend on the total abundance of the organisms in the community composition data.

Due to the differences in the number of trawls per ENSO CATEGORY might introduce bias into these diversity measures (Fig. S3), we calculated the alpha, gamma, and total beta diversity values 500 times by randomly selecting 150 trawls each iteration (i.e., bootstrap). To compare the diversity values between ENSO phases, we performed a pairwise comparison using the Tukey honestly significant test (Tukey 1949) using the bootstrapped values by ENSO category.

2.5. Spatial beta diversity analysis

We first divided the studied area into segments (called ‘segment sites’ hereafter) of one latitudinal degree and 10 NM distance to the coast (Fig. 1 and Fig. S2). Then, we estimated the total beta diversity index (BD_{Total}) for each ENSO category. We also partitioned each total beta diversity index into Local Contributions to Beta Diversity (LCBD). LCBD indices represent the degree of uniqueness of the community composition at a site (i.e., segment site in this case) compared to a vector of mean community composition for all sites (Legendre and De Cáceres 2013). The LCBD indices were calculated as the row sums of the squared deviations from the species mean in the abundance matrix, divided by the total sum of squares. LCBDs were assessed for significance using 9999 permutations (Legendre and De Cáceres 2013). Significant LCBD values indicate segment sites with community compositions that differ from others in each ENSO category. LCBD indices per segment site were calculated for each ENSO category separately, using the beta.div function of the adespatial package in R (Dray et al. 2022). In addition, these LCBD values were plotted by distance to the shelf break (in NM) and intervals of latitude to observe spatially the taxa variation by ENSO category.

We performed a space-constrained hierarchical clustering to identify ecological regions with similar species composition. A constrained clustering method considers i) the information of the dissimilarity

Table 1 (*continued*)

Year	Name	Begin Date (Month)	End Date (Month)	N° trawls	ENSO phase (ICEN)	ENSO phase (ONI)
2007	C0702-04	2	4	137	LN_Strong	N_Summer
	C0708-09	8	9	80	LN_Strong	LN_strong
2008	C0802-04	2	4	96	N_Summer	LN_strong
	C0808-09	8	9	46	EN_Weak	N_Spring
	C0811-12	11	12	67	N_Summer	N_Summer
2009	C0902-04	2	4	82	N_Summer	N_Summer
	C0908-09	8	9	53	EN_Weak	CP_EN
	C0912	12	12	50	N_Summer	CP_EN
2010	C1001-02	1	2	35	N_Summer	CP_EN
	C1002-04	2	4	108	N_Summer	CP_EN
	C1008-09	8	9	33	LN_Mod	LN_strong
	C1011-12	11	12	105	LN_Mod	LN_strong
2011	C1102-04	2	4	117	N_Summer	N_Summer
	C1108-10	8	10	49	N_Spring	N_Spring
2012	C1202-04	2	4	117	N_Summer	N_Summer
	C1209-11	9	11	115	N_Spring	N_Spring
	C1211-12	11	12	31	N_Summer	N_Summer
2013	C1302-04	2	4	125	LN_Strong	N_Summer
	C1308-09	8	9	119	LN_Strong	N_Spring
2014	C1402-04	2	4	134	N_Summer	N_Summer
	C1408-09	8	9	31	EN_Weak	N_Spring
	C1408-10	8	10	129	EN_Weak	N_Spring
2015	C1502-04	2	4	127	N_Summer	CP_EN
	C1508-10	8	10	130	EN_strong	EN_extreme
2016	C1603-04	3	4	134	EN_strong	EN_extreme
	C1605-06	5	6	109	EN_strong	EN_extreme
	C1608-09	8	9	45	N_Spring	N_Spring
	C1609-11	9	11	147	N_Spring	N_Spring
2017	C1703-04	3	4	129	EN_Mod	EN_coastal
	C1708-09	8	9	28	N_Spring	N_Spring
	C1709-10	9	10	142	LN_Strong	N_Spring
2018	C1802-04	2	4	148	LN_Strong	N_Summer
	C1809-11	9	11	174	EN_Weak	CP_EN
2019	C1902-03	2	3	138	N_Summer	CP_EN
	C1909-11	9	11	161	N_Spring	CP_EN

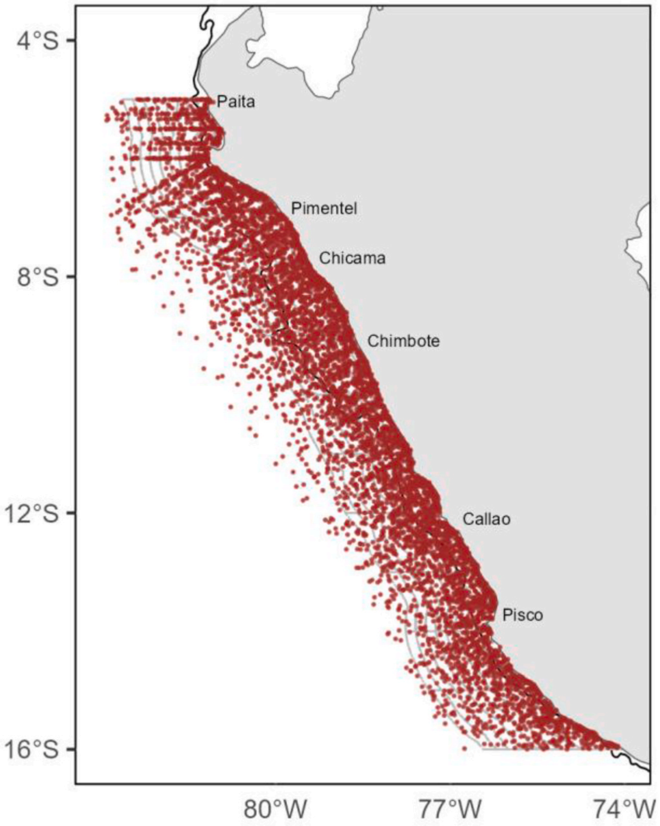

Fig. 1. Trawl points from the pelagic surveys conducted from 1995 to 2019. Grey lines define the 88 segment areas used in our analyses. Only trawls located inside the segment areas were considered for analysis.

matrix computed among segment sites based on the fish composition and ii) the spatial or temporal contiguity information among the segment sites (Legendre and Legendre 2012). Clustering the geographic sites may be carried out from the composition data (as in this study), environmental variables, or any other set of variables observed through space or time. In the clustering of the site composition data, the space-constrained clustering method takes into account the spatial contiguity of the segment sites represented by a list of link edges describing the spatial connecting graph among the sites (Guénard and Legendre 2022) (Fig. S2). The geographical coordinates of the segment sites were used as input to obtain a contiguity matrix of the sites by computing a Delaunay triangulation. The list of link edges was derived from the contiguity matrix and provided to the clustering function, which used it as a constraint during clustering. The Delaunay triangulation criterion, an algorithm of geometric connection (Legendre and Legendre 2012), is an appropriate connecting scheme for space-constrained clustering. Clustering was computed for each of the ENSO categories. For these analyses, we used the constr.hclust function (Guénard and Legendre 2022) available in the R package adespatial (Dray et al. 2022). The clustering method used was Ward's agglomerative method with the constraint of spatial contiguity.

We determined the most characteristic fish taxa among the cluster groups of trawls (i.e., ecological region) through an indicator species analysis. The indicator value index of a species (IndVal (Dufrêne and Legendre 1997; Legendre 2024), is calculated as the product of two quantities, called A and B. Quantity A, or specificity (computed from the species abundance values), measures the strength of a species association with a group of sites. Quantity B, or fidelity, provides information on the relative frequency of occurrence of the species among the sites of a group. The IndVal index is tested for significance through a permutation procedure. This index reaches the maximum value when all individuals of a species are found in a single group of sites, and the species occurs in all sites of that group. The IndVal approach was applied using the function multipatt of the indicspecies R package (De Cáceres and Legendre 2009).

2.6. Temporal beta diversity analysis

We also explored the variability in the composition and structure of the community among ENSO categories using Temporal Beta-diversity Indices (TBI). These indices compare site-by-site data collected in two different periods, T1 and T2. They are composed of two parts for each site: B = species losses and C = species gains for species occurrence or abundance data (Legendre 2019; Legendre and Condit 2019). For our study, the index used was the percentage difference, also known as the Bray-Curtis index. We compared the processes of loss and gain of species abundance (i.e., CPUE) to identify the geographic areas where changes were the most important between the following ENSO categories:

- C1 - T1: N_Summer and T2: N_Spring, to quantify if there was seasonal variability in the abundance of fish species during neutral phases;
- C2 - T1: EN_extreme and T2: EN_strong, to observe how the event's intensity - from extreme to strong - influenced the loss or gain of abundance per species; and,
- C3 - T1: EN_strong and T2: EN_moderate, as in the previous comparison, to look into the EN event intensity - from EN strong to EN moderate.

TBI was computed using the TBI function available in the adespatial R package (Dray et al. 2022). We used the B and C statistics to produce B-C plots, with B (species abundance losses at the site) in the abscissa and C (species abundance gains at the site) in the ordinate. B-C plots show the details of the processes of gain and loss of species through time and across the groups of areas of the northern HCS. We computed B-C plots for each of the comparisons listed above.

To understand the variability of the community structure, we analysed the changes in the 67 taxa across segment sites between each category comparison, using a paired t-test. The tests were conducted with 9999 random permutations of the values in each segment site between T1 and T2. A Holm correction for multiple testing was applied to the computed p-values. The calculations are implemented in function tpaired.krandtest, available in the R package adespatial (Dray et al. 2022).

Finally, because collecting anchoveta information was one of the main goals in the scientific surveys and that species might be overrepresented in our data, we also assessed this potential bias in our results by performing the spatial diversity analyses described above after removing the anchoveta data from the community composition matrix.

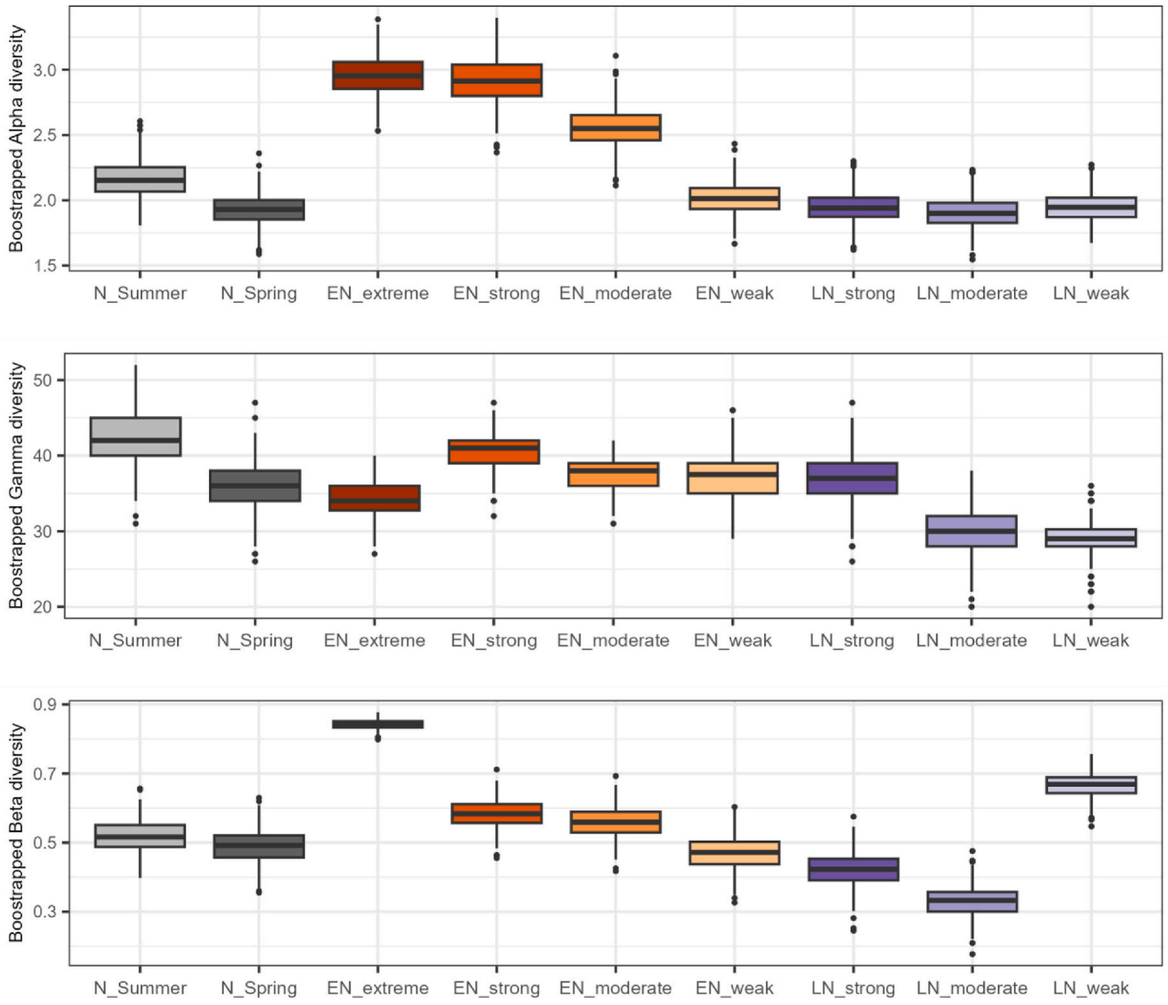

Fig. 2. Bootstrapped alpha diversity (a), gamma diversity (centre) and beta diversity (bottom) values within trawls for each ENSO category: Neutral Summer (N_Summer), Neutral Spring (N_Spring), El Niño extreme (EN_extreme), El Niño strong (EN_strong), El Niño moderate (EN_moderate), El Niño weak (EN_weak), La Niña strong (LN_strong), La Niña moderate (LN_moderate), and La Niña weak (LN_weak). Colour scale codes by ENSO phase: Neutral is grey, EN is red, and LN is purple.

The code to analyse our data can be found at: https://github.com/gallosopl/ENSO_analysis.

3. Results

The main results described in this section follow the ENSO classification by ICEN. Supporting Information - Appendix C briefly describes our results following the classification by the ONI index. In addition, in Supporting Information – Appendix B, we present the results excluding Peruvian anchoveta from the community data matrix considering the ICEN index for the ENSO classification.

3.1. Global analysis

The bootstrapped mean alpha diversity values varied across ENSO categories (Fig. 2), where El Niño phase generally showed higher mean alpha diversity values: EN_extreme = 2.96, and EN_strong = 2.92 (Tukey's test, $p < 0.05$, Fig. S4). Compared with EN_extreme and EN_strong, we found lower mean alpha diversity with LN phases and EN_weak (Turkey's test, $p < 0.05$, Fig. S4). The mean alpha diversity values for the neutral categories were i) N_Summer = 2.16 and ii) N_Spring = 1.93. A similar pattern was observed for the beta diversity values (Fig. 2). The highest mean total beta diversity was observed in the El Niño extreme category (EN_extreme = 0.84) (Tukey's test, $p < 0.05$, Fig. S4), followed by the weak La Niña (LN_weak = 0.67) (Fig. 2), meaning high variability in the abundance of fish taxa among trawls along the study area. For the neutral phases, both mean total beta diversity values were similar: i) N_Summer = 0.519, and ii) N_Spring = 0.490 (Tukey's test, $p < 0.05$, Fig. S4). Finally, for the mean gamma diversity, most of the phases showed a similar tendency (Fig. 2). However, the highest value was observed N_Summer = 42.43, and the lowest for La Niña categories: LN_weak = 29.14, and LN_moderate = 30.05 (Tukey's test, $p < 0.05$, Fig. S4).

3.2. Spatial beta diversity analysis

Local contributions of individual observations to beta diversity (LCBDs) displayed contrasting patterns across space and ENSO categories (Fig. 3). Most sites with LCBD values higher than their respective mean were observed outside the continental shelf for the Neutral and LN phases. The EN_extreme (extreme) event showed evenly distributed LCBD values in all segment sites between the EN categories. In addition, significant LCBD values were observed in most categories, except for EN and LN moderate, and mostly in oceanic segment sites (50–80 nautical miles) (Fig. 3). For EN_weak and LN_strong, these significant sites were observed at higher latitudes (11–16 °S). High and significant LCBD values indicate high taxa composition uniqueness, often related to low species richness (Table S1). However, some significant LCBD sites with more species richness were found in northern areas near the coast (20–40 nautical miles on the continental shelf) for EN_extreme and EN_strong.

Fig. 4 shows the spatially constrained clustering results for all ENSO categories. The EN_weak and the Neutral and LN categories followed a similar spatial pattern. All categories defined an extensive area covering most of the Peruvian coast (group 1) and a small offshore area that differed from category to category in its latitudinal and longitudinal extension (group 2). For the EN_extreme, EN_strong, and EN_moderate, we observed a clear definition of three ecological regions: one near the coast (group 1), one in the north (group 2), and one distant from the coast (group 3).

Table 2 shows the results of the indicator species analysis for each ENSO category. For most categories, except Neutral Spring with no significant indicator species, the Peruvian anchoveta displayed a significant indicator value for group 1. Conversely, the Panama ligthfish (V. lucetia) was associated with the offshore group areas for EN_extreme (group 3) and EN_weak and LN (group 2). During the extreme EN_extreme phase, we observed in the coastal area (group 2) species such as the Peruvian anchoveta, Pacific sardine (Sardinops sagax), and the longnose anchovy (Anchoa nasus) (Table 2). Also, for EN_extreme, the chub mackerel (Scomber japonicus) was an indicator of groups 1 and 2.

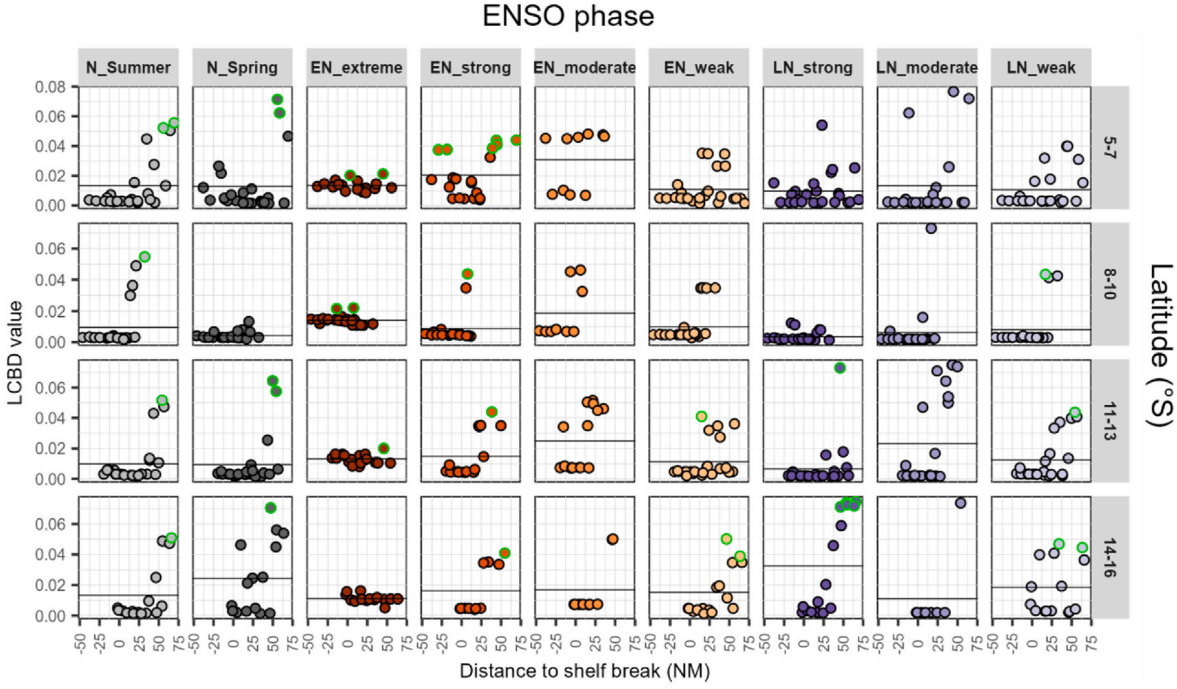

Fig. 3. LCBD index values are computed separately for each ENSO phase. Within each graph, LCBD values are dispersed by distance to the shelf break and latitude. Green dots indicate the significant ($p < 0.05$) LCBD with a permutation test. The black horizontal line represents the mean LCBD value in that graph. The negative values in the distance to the shelf break represent the distances of the segment areas to the shelf break on the continental shelf.

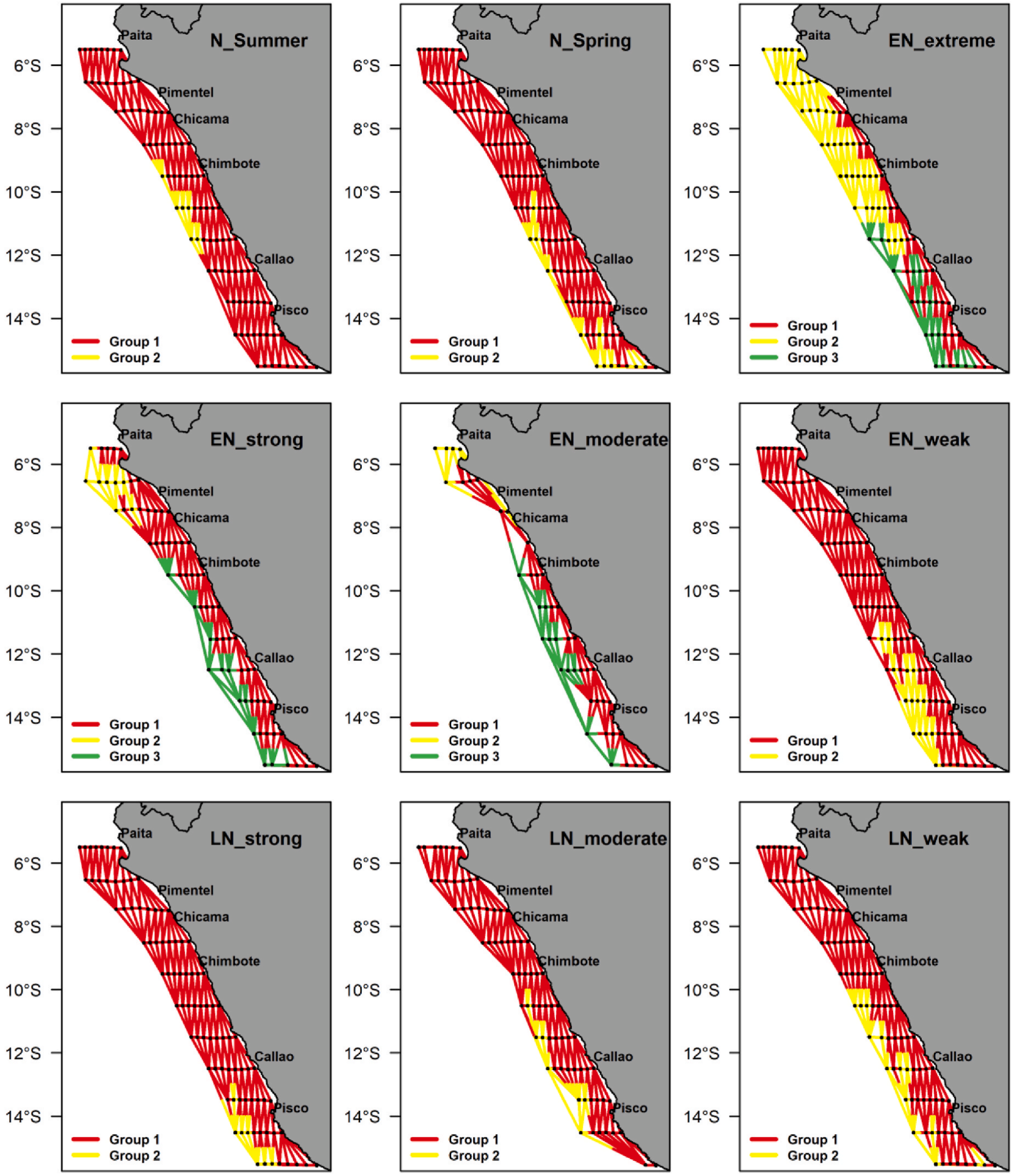

Fig. 4. Space-constrained clustering was used to group areas of similar species composition in pelagic fish taxa during each ENSO category. Clustering method: Ward's minimum variance with spatial contiguity constraint.

Between LN categories, jack mackerel (Trachurus murphyi) was observed for LN_moderate as an indicator species of the offshore area (group 2). The neutral Spring phase did not show an indicator species.

3.3. *Temporal beta diversity analysis*

The temporal beta diversity index (TBI) from the Neutral Summer (T1) to Neutral Spring (T2) phase varied along the study area, with a mean of 0.479. Latitudinally, we observed higher TBI mean values in segment areas of northern (5°S to 7°S – TBI = 0.513) and southern (14°S to 15°S – TBI = 0.566) latitudes (Fig. S5). This variability in composition between neutral categories was related to the high loss of abundance of fishes over all sites (78 % of sites with species losses and 22 % with species gain). In the B-C plots (Fig. 5), the green line is above the black line, meaning a loss of dominance from Neutral Summer to Neutral Spring. Besides, higher TBI values with a gain of abundance-per-taxa were observed in offshore sites – from 50 to 80 nautical miles and northern latitudes 5°S to 7°S (Fig. S5). We observed that the Peruvian anchoveta and the Peruvian silverside (Odontestes regia) significantly changed between neutral categories and showed a drop in their abundance in the Neutral Spring category (Fig. 6).

When comparing the El Niño categories – T1: EN_extreme and T2: EN_strong; the mean TBI value of the whole area was 0.824. Along latitude intervals, TBI values showed less variability (Fig. S5). In this comparison, 59 % of the sites experienced abundance loss per species. The B-C plot (Fig. 5) showed a loss of abundances-per-taxa (the green

Table 2
Indicator species for the pelagic fish community of the northern HCS. For each phase of the study, only the indicator species that are significant indicators at ($\alpha = 0.05$ after 99999 permutations) are shown in order of decreasing IndVal values, where IndVal = A × B. A is the specificity of the species for the group (based on Fig. 4), B is the fidelity or sensitivity of the species. Neutral Spring had no significant indicator species.

ENSO pahase	Taxa	Group	IndVal	A	B
N_Summer	E.ringens	1	0.948	0.996	0.951
EN_extreme	E.ringens	1	0.911	0.997	0.913
	S.sagax	1	0.681	0.979	0.696
	A.nasus	1	0.432	0.903	0.478
	V.lucetia	3	0.693	0.693	1.000
	S.japonicus	1 + 2	0.670	0.997	0.672
EN_strong	E.ringens	1	0.998	0.998	1.000
EN_moderate	E.ringens	1	0.998	0.998	1.000
EN_weak	E.ringens	1	0.864	0.956	0.904
	V.lucetia	2	0.823	0.823	1.000
	Myctophidae	2	0.688	0.875	0.786
LN_strong	E.ringens	1	1.000	1.000	1.000
LN_moderate	E.ringens	1	0.973	0.988	0.985
	T.murphyi	2	0.713	0.998	0.714
LN_weak	E.ringens	1	0.955	0.997	0.958
	V.lucetia	2	0.948	0.948	1.000

line is below the black line). Species such as the Pacific sardine, jack mackerel, chub mackerel, and Panama lightfish (V. lucetia) had a significant loss of abundance with nearly zero abundance values during the EN_strong compared with the EN_extreme (Fig. 6). Otherwise, the Pacific harvestfish (P. medius) was also significant and experienced a gain in abundance values during EN_strong.

The comparison between T1: EN_strong and T2: EN_moderate showed a mean TBI value of 0.563. Northern sites (from 5°S to 7°S) had larger TBI values (Fig. S5). In addition, we observed that 62 % of the total sites had an abundance loss per taxa. In Fig. 5, the B-C plots showed a decrease in abundance-per-taxa (i.e., the green line is below the black line), indicating that significant change in the abundance-per-taxa occurred from EN_strong to LN_strong phases. The Pacific seahorse (H. ingens) was a significant taxon that showed a crucial change in its abundance values (Fig. 6).

4. Discussion

We explored the impacts of ENSO phases on the pelagic fish of the northern HCS. We used a long-term taxonomic dataset collected by scientific surveys and covering several ENSO events, offering unique insights into the variation of fish taxa through space and time. Our findings revealed seasonal differences in taxonomic richness and ecological uniqueness among ENSO phases and magnitude. Higher diversity was observed during EN phases, characterised by a specific spatial structure of the community that varied in extent, species indicators and composition among EN categories. The most remarkable changes in temporal beta diversity were observed when the system transitioned from a neutral to the EN phase, where the loss in abundance per fish taxa was the dominant process. In the following paragraphs, we discuss the influence of environmental and population variables on our results, the limitations of the dataset and their potential impacts on our results, the importance of our findings, and outline future studies that could enhance our understanding of fish dynamics in the northern HCS.

EN extreme, strong and moderate categories displayed the larger mean diversity indices, where the EN_extreme reported the maximum values. This increase in local diversity can be attributed to the system dynamics experienced during this phase. Specifically, during EN events, the system is generally characterised by a warmer and nutrient-poor environment (Espinoza-Morriberón et al. 2017, 2025; Mogollón and Calil 2017), primarily due to a reduction in upwelling (Bertrand et al. 2020). In addition, the southward movement of tropical water masses and the decrease in the extension of cold coastal waters (Swartzman et al. 2008) may provoke the introduction of tropical species to southern regions and oceanic species closer to the coast (Ñiquen and Bouchon 2004), thereby producing an increase in the number of species inhabit our study area (Chavez et al. 2008). Furthermore, we observed significant differences in beta diversity values for the four El Niño categories (extreme, strong, moderate and weak), increasing values progressively from weak to extreme EN phases. These results suggest that the spatial structure or change in the species abundance along the northern HCS is

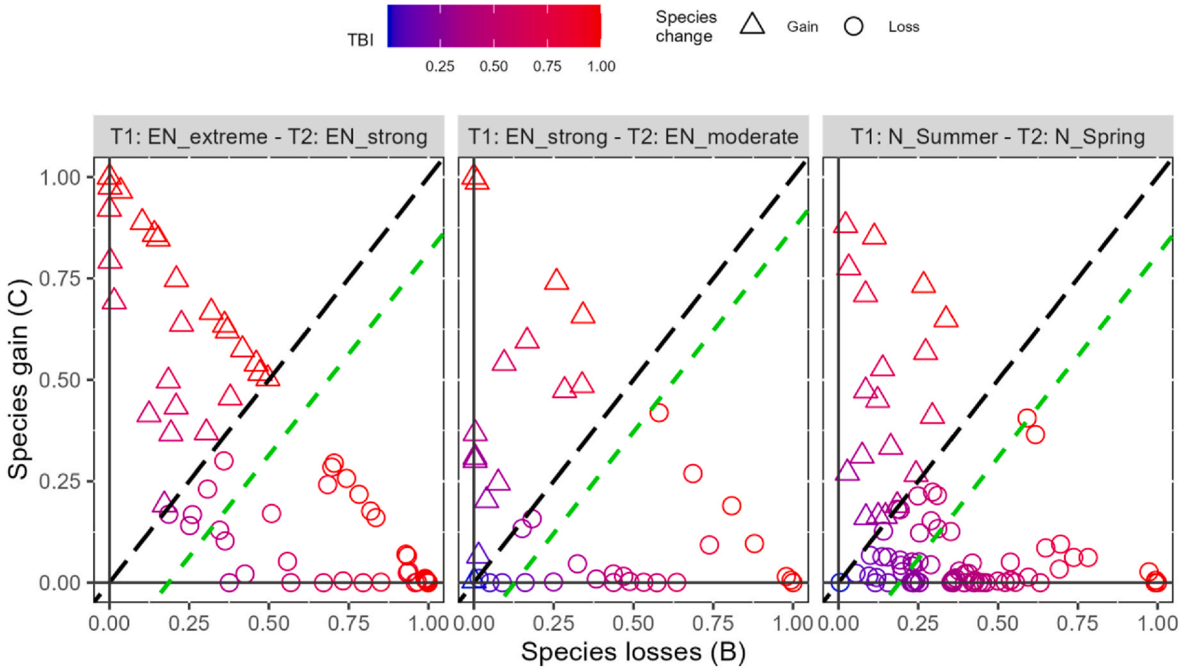

Fig. 5. B-C plots of species abundance data compared between two ENSO phases. Symbol diameters are proportional to TBI statistics. The black line with a slope of 1: the line where gains equal losses. The green line is drawn parallel to the black line and passes through the point centroid. Symbol colours represent the TBI statistic values from o (dark blue) to 1 (bright red).

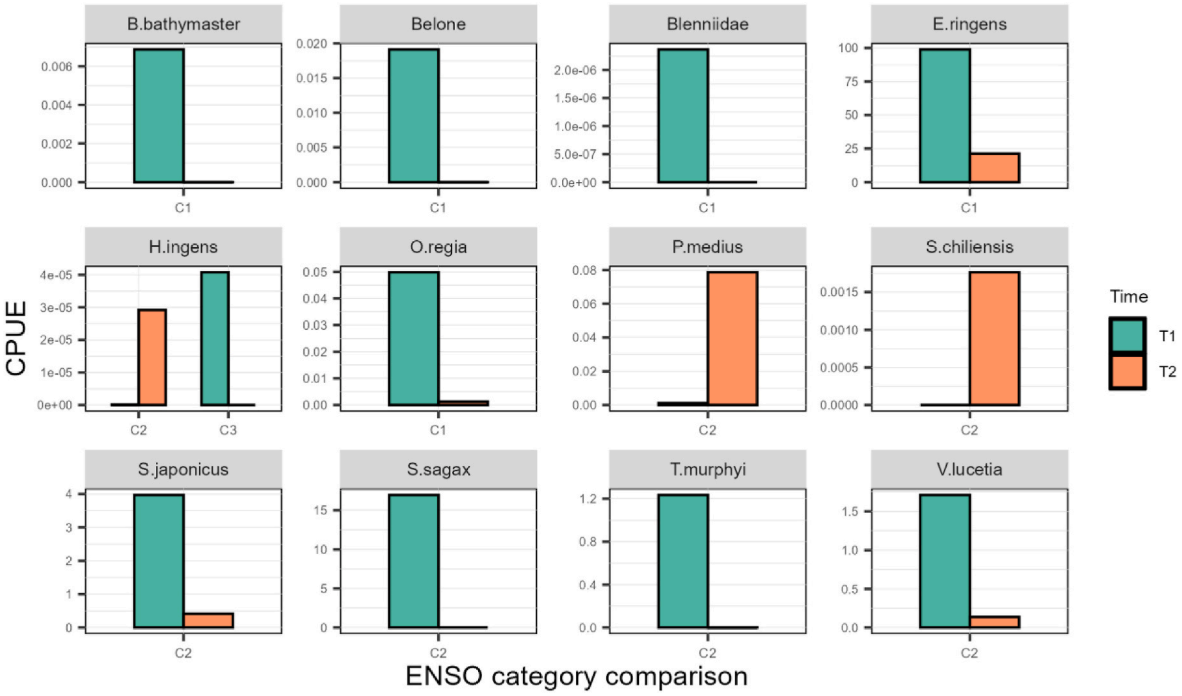

Fig. 6. Species that significantly changed in abundance. Bar colours represent either T1 (green) or T2 (orange) in the comparisons of ENSO categories. CPUE: catch per unit effort (Kg/min) as abundance index. ENSO categories comparison - C1: T1-N_Summer and T2-N_Spring, C2: T1-EN_extreme and T2-EN_strong, C3: T1: EN_strong and T2:EN_moderate.

influenced by the magnitude of the El Niño phase: a higher magnitude produces larger impact on the spatial structure of the community.

The case of EN_weak is particularly noteworthy, as its diversity metrics are comparable to those observed during neutral categories (summer and spring), indicating minimal impact on community structure. Considering the global ENSO classification by ONI, some EN weak events correspond to Central Pacific (CP) EN (Table 1). It has been reported that due to its characteristics, CP EN events do not always result in HCS impacts (Bertrand et al. 2020), even producing negative sea surface temperature anomalies along the Peruvian coast (Timmermann et al. 2018; Lehodey et al. 2020). Conversely, the La Niña categories produced the opposite effect compared to EN, showing the lower alpha and gamma diversity among the ENSO phases. During LN events, cold coastal waters extend over the Peruvian coast, increasing upwelling and nutrient concentration (Espinoza-Morriberón et al. 2025), extending the spatial distribution of some species with affinity to cold coastal waters such as Peruvian anchoveta (Moron et al. 2019), and such establishing a more homogeneous system with less diversity.

Significant LCBDs are located at sites beyond the continental shelf and mainly in areas with low richness for most of the ENSO phases. These patterns are usually expected because they indicate that the high uniqueness of species composition can often be related to a low number of species which are maybe specialised and tolerant to distintive conditions (Legendre and De Cáceres 2013), not necessarily associated with the characteristic of the fish taxa in the northern HCS. However, for the extreme and strong EN categories, we also observed significant sites with higher richness located in northern regions (5°S to 10°S latitude) and closer to the coast (10–30 NM), reflecting the inclusion of novel species (e.g. migratory species) in the community during warm periods. In addition, research on marine diversity has described that coastal areas are often characterised by higher species richness than oceanic areas due to their diverse habitats and higher productivity (Tittensor et al. 2010). No significant LCBD sites were observed during both EN and LN moderate categories, meaning that the regional variability is constant during these phases and does not have a particular unique taxonomic characteristic.

Understanding the spatial patterns of biological communities helps us learn about system dynamics and how communities are organised across varying environments (Baker and Hollowed 2014). We noticed differences in how the fish community spread geographically during different ENSO phases. During the Neutral phase (in summer and spring) and weak El Niño and La Niña categories, the communities appeared similar in their spatial arrangement. However, during the extreme, strong, and moderate El Niño categories, we observed that the northern HCS is divided into three main areas, each with a similar community composition (ecological regions), and these areas changed in spatial extension during these categories. The layout of these areas relates to how water masses are distributed in this ecosystem (Zuta and Guillén 1970) and how they vary during El Niño events (Swartzman et al. 2008). Our results show that the intensity of the EN is crucial to defining the spatial structure of the community. An EN extreme is characterised by intense warming over the most equatorial Pacific due to the extension of tropical water masses from the north and a higher contraction of the cold water masses further to the coast (Swartzman et al. 2008).

The indicator species for each ENSO phase help us understand the changes in fish biodiversity during warm and cold periods. For all ENSO phases, the Peruvian anchoveta is an indicator of the region located closer to the coast or the region covering most of the northern HCS. The Panama lightfish also acts as an indicator in oceanic areas. These two species define geographical areas and might be influenced by the shelf break since the Peruvian anchoveta primarily dwells in neritic environments (Moron et al. 2019) while V. lucetia prefers offshore areas (Cornejo and Koppelmann 2006), so it is uncommon to find both species in high numbers in the same region. During the EN_extreme category, the chub mackerel was also an indicator for the regions that covered both the northern and coastal part of the study area. This result agrees with the findings from Espino (1999) and Ñiquen and Bouchon (2004), which described that during the El Niño event of 1997-98, many oceanic and tropical species, like mackerels, tunas, and billfishes, moved from north to south. The small proportion of species showing preferences during the EN strong, moderate and weak categories, compared to the El Niño extreme, may be due to this event’s high variation and perturbation in 1997-98 in the northern HCS system.

The El Niño and La Niña phases trigger contrasting species' behaviour and fisheries responses (Chavez et al. 2008; Bertrand et al. 2020; Lehodey et al. 2020). On average, during El Niño, the total landings in the northern HCS decrease, while they increase during La Niña events, mainly caused by the changes in biomass of the Peruvian anchoveta (Bertrand et al. 2020). When comparing the EN extreme and strong categories, we observed a significant and similar decline in abundance-per-taxa in all segment areas as observed for the Pacific sardine and jack mackerel. One of the main drawbacks when comparing taxon-specific abundance between two categories is that other factors (e.g., fishing, long-term variability) besides the studied one may impact the outcome. For example, for the Pacific sardine the increase in fishing pressure in the late 1990s has been associated with this species' drastic decline in abundance after 1999 (Cárdenas-Quintana et al. 2015), provoking the disappearance of this species in the northern HCS since then. Therefore, it is unlikely to see this species flourish in a near-future extreme EN event. For jack mackerel, the decrease in biomass coincided with the removal of larger individuals during a period of high fishing effort in the late 1990s (Gerlotto et al. 2012), which might also suggest a significant effect of fishing (Hintzen et al. 2014). In addition, there is evidence of changes in average ocean conditions from the late 1990s (i.e., regime shift), which impacted the dominance of the main pelagic fishes in the northern HCS (Alheit and Ñiquen 2004). Therefore, this long-term fluctuation might have impacted our results when comparing ENSO categories before and after 2000.

4.1. Caveats

This study uses taxonomic data collected by scientists through a standardised survey over several years. This survey is the best source for understanding changes in the fish community in the northern HCS. Other data sources, like fisheries catch data, can provide insights but have limitations. Catch data spans a long period but is influenced by gear type, fishermen's behaviour, and market prices, all of which affect the types of fish caught. While acoustic data from scientific surveys can show the abundance of some species, it is only available for a few taxa (Castillo et al. 2009). Global datasets, such as OBIS, can provide information on fish diversity, but they lack the time detail needed for this study's analysis.

Although the data used in this study is appropriate, we must recognise some flaws in the sampling protocol that could affect our results. The primary issue is the tendency to do the trawl sampling where anchoveta was likely present, implying the possibility of over-representing areas where other species may have been present. However, we covered the entire study area for all ENSO phases (Fig. S3). Another limitation is the taxonomic resolution for certain fish taxa. Although trained fishery biologists did the identification, some rare species were difficult to classify at the species level. To mitigate this, we standardized the taxonomic information with input from experienced scientists at IMARPE, creating a comparable dataset of fish taxa across surveys (Supp Information – Appendix A).

Additionally, while CPUE may not accurately reflect abundance for some species due to differences in catchability, we believe this does not affect our conclusions comparing different ENSO phases since this effect is consistent across surveys. Finally, we had higher sampling in coastal areas (within five nautical miles). Although this led to variability in the number of trawls performed near the coast, our resampling results helped us understand diversity differences between ENSO categories without focusing on how diversity patterns change with distance from the coast.

5. Conclusions

Our analysis provides insights into the community structure of pelagic fishes in the northern HCS and suggests that ENSO phases affect the spatial structure of the community, resulting in higher alpha and beta diversity values and a more heterogeneous community during the El Niño extreme and strong phases, with a higher abundance of tropical and oceanic species. In addition, we observed that during EN phases, the northern HCS pelagic fish community can be spatially structured into three ecological regions with similar community composition. We also identified indicator species of ecological regions during the various ENSO phases. Understanding the functioning of the northern HCS diversity is essential to appropriately manage this highly productive system within an ecosystem-based management framework.

CRediT authorship contribution statement

Paola Galloso: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Giancarlo M. Correa:** Writing – review & editing, Supervision, Methodology. **Pierre Legendre:** Writing – review & editing, Supervision, Methodology, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr2.2025.105553.

Data availability

The authors do not have permission to share data.

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